

Global biodiversity and life-history evolution in the proso-branch gastropods

Biodiversidad global e historia evolutiva en los gasterópodos proso-branquios

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ABSTRACT

Description of biodiversity over its spatial dimension must be accomplished under many perspectives, including ecological, physiological and functional characterisation, and requires a profound understanding of the dynamic processes producing biodiversity. Marine gastropod molluscs, owing to their biphasic life-cycles, and the alternative (planktotrophy vs. non-planktotrophy) larval strategies recorded in their shells (particularly in the caenogastropods), are a very suitable group to study evolutionary processes related to temporal and spatial patterns of biodiversity. The differences in life strategies often result in different speciation patterns: I. Speciation within groups with planktotrophic larval development (mainly peripatric). II. Speciation within groups with non-planktotrophic development (usually supported by the reduced or absent gene-flow). III. A "transversal" model of speciation involving loss of planktotrophy as a leading factor. Pairs of sibling "species" differing mainly or only in their developmental strategy are known from all oceans although they have been particularly well studied in the Mediterranean Sea. Indo-Pacific cases from the families Muricidae and Conidae are herein reported. Alternative developmental phenotypes produced by heterochrony provide an "Alternative adaptation" basis for evolution. Quaternary paleoclimatic fluctuations can probably be considered among the main factors having affected marine, land and freshwater assemblages, producing the present patterns of biodiversity.

RESUMEN

La descripción de la biodiversidad en su dimensión espacial debe enfocarse desde varias perspectivas, que incluyen la caracterización ecológica, fisiológica y funcional, y requiere, además, un profundo conocimiento de los procesos dinámicos que la producen. Los moluscos gasterópodos marinos, con sus ciclos vitales bifásicos y con las estrategias larvarias alternativas de planctotrofia vs. no-planctotrofia, que queda registrada en sus conchas, principalmente en los caenogasterópodos, son un grupo muy adecuado para estudiar los procesos relacionados con los patrones de biodiversidad temporal y espacial. Las diferencias en los ciclos vitales dan lugar, frecuentemente, a diferentes pautas de especiación: I. Especiación dentro de grupos con desarrollo planctotrófico (sobre todo peripatrica). II. Especiación dentro de los grupos que carecen de desarrollo planctotrófico (gene-

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ralmente basada en un flujo génico reducido o ausente). III. Un modelo "transversal" de especiación que conlleva la pérdida de planctotrofia como el factor dominante. Se conocen parejas de "especies" hermanas que difieren sobre todo o únicamente en sus estrategias de desarrollo. Estas "especies" se han hallado en todos los océanos pero han sido particularmente estudiadas en el mar Mediterráneo. También se tratan aquí algunos casos Indo-Pacíficos de las familias Muricidae y Conidae. El desarrollo de fenotipos alternativos producidos por heterocronía proporcionan las bases de una "adaptación alternativa" para la evolución. Las fluctuaciones paleoclimáticas cuaternarias pueden probablemente considerarse como uno de los principales factores que afectaron a las comunidades marinas, terrestres y dulceacuícolas, produciendo los patrones actuales de biodiversidad.

KEY WORDS: Biodiversity, life-histories, evolution, speciation, larval ecology, Indo-Pacific, North East Atlantic.

PALABRAS CLAVE: Biodiversidad, ciclos vitales, evolucion, especiacion, ecologia larvaria, Indo-Pacifico, NE Atlantico.

INTRODUCTION

Conservation of Biodiversity is the topic of this century's end. It requires a more than good knowledge of the patterns of biotic diversity in land and aquatic environments. Gaining this knowledge is not a simple task. Description of biodiversity across its spatial dimension is presently accomplished under many perspectives, including ecological, physiological and functional characterisation. This approach and the results of the recent advances in taxonomy produced figures of diversity three to five times greater than previously recognised (KNOWLTON AND JACKSON, 1994; KNOWLTON, 1993), particularly with the discovery of a high number of sibling/cryptic species. To get a deeper understanding of the dynamic processes producing biodiversity we have to cope with important components operating over a temporal scale. The availability of ecological, physiological and morpho-functional descriptors for species and communities is of great advantage in these evolutionary studies. The life-histories of the organisms involved play an important role for the understanding of the evolutionary processes. Particularly, larval ecology (long vs. short/absent pelagic life) exerts a remarkable influence on the life history of a species (dispersal capability, possibility and the extent of gene

flow between populations, extinction/speciation rate, etc.: MILEIKOVSKY, 1971; SCHELTEMA, 1972, 1977; SHUTO, 1974; VALENTINE AND JABLONSKI, 1986; HEDGECOCK, 1986). Thus, admittedly larval development is correlated with temporal aspects of the evolutionary history of the invertebrates (VALENTINE AND JABLONSKI, 1986).

Marine gastropod molluscs are a very suitable group to study life-histories and evolutionary processes related to temporal and spatial patterns of biodiversity: they are important contributors to biodiversity patterns and can be easily studied throughout their life-histories. Like most of the marine invertebrates (JABLONSKI AND LUTZ, 1983; STRATHMANN, 1978a, 1978b, 1985), in their biphasic life cycles several developmental strategies have been adopted by the marine prosobranchs that can fall into two fundamental categories:

[P] planktotrophic development, with larvae feeding on plankton, spending a relatively long time in the planktonic stage;

[NP] non-planktotrophic development: in the major part lecithotrophic (but including also direct development, brooding etc.): larvae, if present (lecithotrophic), have at their disposal a more or less large yolk supply, reach metamorphosis without feeding on plankton and

usually spend less time than P-larvae or no time at all in the plankton. Dissolved organic material uptake can be an additional source of energy (see MANAHAN, 1990; JAECKLE AND MANAHAN, 1989) but this does not affect the present dichotomous scheme.

Features of embryonic/larval shells (protoconchs) are powerful tools to identify the mode of development of each individual; if the protoconch is preserved in the adult, the larval development can be inferred from characteristics of the sculpture and by comparison of the dimensions (THORSON, 1950; JABLONSKI AND LUTZ, 1980; LIMA AND LUTZ, 1990; BANDEL, 1982). The developmental type of specimens in fossil material can be also defined, when the protoconchs are preserved. It is a rare possibility in the Animal Kingdom, that allows one to study this biological feature along a temporal dimension (though caution must be used to avoid abuse: BOUCHET, 1990).

The differences in life strategies are thought to result in different speciation patterns:

I. Speciation within groups with planktotrophic development. Speciation usually occurs at the edges of the ancestral species' range (HANSEN, 1978; SHUTO, 1974); often a peripatric model (MAYR, 1982) could explain the speciation events, notwithstanding the alleged homeostatic effect of the larval dispersal. A similar model has been proposed by REID (1986) for the genus *Littoraria* (fam. Littorinidae). A good example can be seen also in the cones of the group of *C. textile* L. 1758. *Conus textile* is rather uniform morphologically within its range, with the exclusion of the edges, the Western Indian Ocean (RÖCKEL, KORN AND KOHN, 1995) and the Eastern Pacific Ocean, where examples such as *C. textilinus* Kiener, 1845 from the Marquesas and the closely related *C. dalli* Stearns, 1873, from the Panamic region indicate the various levels of differentiation of the peripheral pools, contrasted by the homogeneity within the range. *Conus namocanus* Hwass in Bruguiere, 1792 (from the Western Indian Ocean) overlaps with the

western part of the range of the related *C. capitaneus* L., 1758, both having a planktotrophic larval development.

II. Speciation within groups with non-planktotrophic development. Usually due to the reduction or even absence of gene flow between populations (low dispersal capability), speciation appears like a classic allopatric event, and in some conditions, radiation may be favoured because of the isolation of the demes. The case of the rissoids of the genus *Manzonina* in the Macaronesian archipelago is just one case among the others (MOOLENBEEK AND FABER, 1987a, 1987b, 1987c).

III. Speciation associated with the loss of planktotrophy (OLIVERIO, 1991, 1994a, 1995b). This "transversal" model of speciation is supported by the existence of pairs of sibling species, differing only or mainly in their larval development. Its mechanism involves the modification of larval development with the loss of planktotrophy as a leading factor. Environmental factors can be responsible for switching off the pelagic larval phase in specific conditions that select against planktotrophs. Restricted areas, higher predation rate, changes in food availability, etc., can be considered as the main factors (STRATHMANN, 1978a, 1978b).

The phenomenon of the pairs of sibling "species" differing mainly or only in developmental strategy has been particularly studied in the Northeast Atlantic where an increasing dominance of the NP mode going eastward in the Mediterranean basin has been scored (OLIVERIO, 1997). Levels of genetic divergence, based on allozymic data in a few case-studies (OLIVERIO, 1994b, 1995a; MUNKSGAARD, 1990) address relatively recent events of separation of the entities within each pair (ca. 2 MY bP in the case of the pair *Columbella adansonii*/*C. rustica*; 250.000 to 5.000 years for some rissoid pairs).

In the NE Atlantic area some Recent species with non-planktotrophic development are indisputably related to ancestors displaying protoconchs of the planktotrophic type. The analysis of

some such lineages revealed that most of the P>NP transitions are located between the Pliocene/Pleistocene boundary and the Middle Pleistocene (OLIVERIO, 1994a). Genetic data that address very recent events of separation in some pairs support the idea that marine faunal assemblages have been strongly affected by the Quaternary palaeoclimatic fluctuation, that in some cases were actually dramatic (ANTONIOLI AND OLIVERIO, 1996).

Some implication of the differences in the larval strategies of some gastropods have been already discussed (BOUCHET, 1989), and it is known that variation in larval development is not exclusive to molluscs (HOAGLAND AND ROBERTSON, 1988). It is here stressed that even for gastropod molluscs this is a world wide phenomenon. Examples of pairs of sibling species, or of species-complexes, where the evolution of the larval development played a crucial role in their diversification, can be observed even at first sight in the major families of caenogastropods (see e.g. SAFRIEL AND HADFIELD, 1992).

In the family Muricidae, *Murex tribulus* L. 1758, is a common species in the Indo-West Pacific and has a planktotrophic larval development, whilst its sibling *Murex forskaeli* Lischke, 1868, is restricted to the Red Sea, the Arabian Sea and adjacent areas and has a non-planktotrophic larval development (PONDER AND VOKES, 1988). *Naquetia triquetra* (Born, 1778) occurs mainly in the Western Pacific Ocean and is recorded westward till Christmas Islands in the Indian Ocean: it has a planktotrophic larval development. *Naquetia cumingi* (A. Adams, 1853) has the same range in the West Pacific and extends in the Indian Ocean till the Southern Red Sea and the Eastern African coasts (HOUART, 1992): it has a non-planktotrophic larval development. In analogy to what occurs in the Northeast Atlantic, the pairs are more easily scored in the more diverse families. The neogastropods Conidae (s.s.) are an excellent subject to study biogeographical patterns of life-history evolution (KOHN AND PERRON, 1994). In

Madagascar cones of the *C. textile* group are known that, according to larval shell dimensions, probably have a non-planktotrophic larval development (G. Raybaudi, pers. comm.). *Conus omaria* Hwass, 1792 is distributed through the Indo-West Pacific and has a planktotrophic larval phase, that is missing in the development of its counterpart, *C. madagascariensis* Sowerby II, 1858, from India. *C. aureus* Hwass, 1792 is known from the Indo-West Pacific (excluding the Red Sea and the Arabian Sea) and has a planktotrophic larval development, while the non-planktotrophic *C. barbieri* Raybaudi, 1995 is endemic to the Philippines. *C. capitaneus* L., 1758 (with P larval phase) has a sibling along the Northern Australian coasts with non-planktotrophic larval development, viz. *C. trigonus* Reeve, 1848. *C. inscriptus* Reeve, 1843 with planktotrophic development ranges from Vietnam to the Western Indian Ocean: its recently described sibling *C. salzmanni* Raybaudi AND Rolán, 1997 is presumably endemic to the Aden region and has non-planktotrophic development.

It appears that the model of Speciation III can be easily exported from the NE Atlantic region to the entire marine realm. The discovery of a high number of sibling/cryptic species in the tropical environments, that greatly increased the known figures of diversity (KNOWLTON AND JACKSON, 1994; KNOWLTON, 1993), means that these diversity patterns are probably the results of very recent (and correlated) events of speciation. Taking into consideration the importance of the evolution of life-histories when linked with palaeoclimatic fluctuations, in driving rapid evolutionary transitions, models such as Speciation III can help understanding the present patterns. The Recent evolution of highly diverse marine environments such as the tropical ones, should probably be reconsidered in terms of alleged stability vs. sensitivity to (palaeo-)climatic fluctuations.

The genetics of characters related to either planktotrophy or lecithotrophy in a "poecilogonic" polychaete have been discussed by LEVIN, ZHU AND CREED

(1991) from an evolutionary perspective. STRATHMANN, FENAUX AND STRATHMANN (1992) observed heterochronic developmental plasticity in a sea-urchin. Heterochrony is suggested to be an important prerequisite for evolutionary developmental transitions; it can explain the (presumably intraspecific) variation observed in some cases. Changes in timing (speed and sequence) of the developmental pathways underlie many aspects of organismal diversity (GOULD, 1977; MCKINNEY, 1988; RAFF, PARR, PARKS AND WRAY, 1990). Yet, little is known about the mechanisms ruling heterochronic variations (BLACKSTONE AND BUSS, 1993; PARKS, BISGROVE, WRAY AND RAFF, 1993), and only recently theoretical models for the reaction norm are being tested (GAVRILETS AND SCHEINER, 1993 a, b). Heterochronic changes in genes operating during oogenesis can result in changes (even dramatic ones) in the developmental pathway. According to STRATHMANN *ET AL.* (1992) heterochrony can account for at least the initial transition to non feeding larval development. Alternative developmental phenotypes produced by heterochrony thus provide an "alternative adaptation" basis for evolution (WEST-EBERHARD, 1986; SMITH-GILL, 1983). Heterochrony, an important prerequisite to many evolutionary developmental modifications, can account for at least the initial transition to non feeding larval development. Planning experimental studies in this ambit requires to accept as working hypotheses odd and controversial evolutionary models (e. g. genetic assimilation), to be read in the modern context of the reaction norm (GAVRILETS AND SCHEINER, 1993a, b). Environmental factors operating over this epigenetic plasticity should pro-

bably be searched for in the ambit of paleoclimatic changes (with all correlated events: sea-level and temperature, coastline and water current modifications, etc.). Quaternary paleoclimatic fluctuations are normally regarded as the main factor having affected land and freshwater biodiversity. Their effects also on the marine assemblages are probably not fully acknowledged.

CONCLUSIONS

Everyone knows that studying biodiversity is a matter of synthesis and requires comprehensive knowledge of basic science. The case of the evolution of larval development highlights how morpho-functional descriptors must be taken into consideration while describing spatial pattern of biodiversity, since they bear information on the temporal aspects (dynamics) underlying the biotic diversity evolution. Probably, very recent events significantly contributed to produce present biodiversity patterns, that is: Evolution runs fast, sometimes faster than we imagine. Heterochronic changes in the early ontogeny, when life histories of the species are "encoded", can easily contribute to this scenario.

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